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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE
FAUNA. XII. THE POSTCRANIAL SKELETON
OF THE THECODONT *CHANARESUCHUS*.

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ABSTRACT. A description is given, with a reconstruction, of the postcranial skeleton of the long-snouted thecodont *Chanaresuchus bonapartei* from the early Middle Triassic Chañares Formation of Argentina. The general proportions are comparable to those of crocodilians, and life habits may have been similar. However, there is no positive indication of relationship to either later Crocodilia or Phytosauria, and *Chanaresuchus* and its relatives (Proterochampsidae) appear to be a sterile offshoot of the primitive proterosuchian stock. Dermal armor is little developed; the pelvis, although somewhat advanced in build, shows no trend toward the crocodilian elimination of the pubis from the acetabulum; the pes is of a specialized nature, with emphasis on the inner digits.

INTRODUCTION

In a recent paper in this series (Romer, 1971), I described the cranial anatomy of two long-snouted thecodonts, *Chanaresuchus bonapartei* and *Gualosuchus reigi*, from the (? Anisian) Triassic Chañares Formation of Argentina. Few postcranial remains of *Gualosuchus* are available to me. For *Chanaresuchus*, however, a number of specimens from our 1964-65 expedition are at hand, and Sr. Bonaparte allowed me to study several further specimens in the Instituto Lillo of Tucumán collections. Below, I give a description, with restoration, of the postcranial skeleton of *Chanaresuchus*.

Materials. The following specimens from the La Plata-Harvard expedition include postcranial remains:

The holotype: (La Plata Museum 1964-XI-14-12) Skull, partial column, a few limb bones.

MCZ 4035. Part of the contents of a large nodule, including a column articulated to caudal 3, and considerable girdle and limb material.

MCZ 4036. The remainder of material in this nodule, including incomplete and in part poorly preserved remains of skulls and postcranial materials of two further individuals.

MCZ 4037. A skull and presacral column.

MCZ 4038. A slab containing a mélange of materials; most, however, appear to belong to a nearly completely disarticulated *Chanaresuchus* skeleton.

There is considerable variation in the size of the individuals concerned. Largest is MCZ 4037, in which skull length to the quadrate is 260 mm. In the type skull this measurement is 211 mm. My figures of postcranial material (including restoration) are based mainly on MCZ 4035, in which postcranial vertebrae and limb bone measurements indicate a size approximately that of the type. The two skulls somewhat imperfectly preserved in MCZ 4036 measure about 230 and 220 mm. The imperfect skull with which the array of postcranial material on MCZ 4038 appears to be associated had a length of approximately 165 mm.

Several specimens in the Instituto Lillo collections were studied. Best was a specimen with articulated column extending to the proximal part of the tail, and much of the appendicular skeleton; the skull measured, to quadrate, 175 mm, and the individual was thus considerably smaller than the type. A second specimen included much of the postcranial skeleton of a moderately large individual; the skull is missing, but comparison of limb bone measurements indicate a size slightly larger than MCZ 4035. A third Tucumán specimen is an immature individual, in which postcranial measurements are about half those of the type; preserved is a hind foot exactly duplicating the peculiar structure, and a nearly complete tail.

Vertebral column. The atlas-axis complex, best seen in MCZ 4037 (Fig. 1, *a, b*), is of a type readily derivable from that of primitive reptiles. The atlas neural arches are paired. Dorsally a posterior extension was applied to the lateral surface of the axis arch; an anterior extension is flattened ventrally, presumably for articulation with the exoccipital (no pro-atlas has been found). A slight rugosity seen on one specimen indicates a rib attachment. Ventrally the stem of the arch extends stoutly downward to

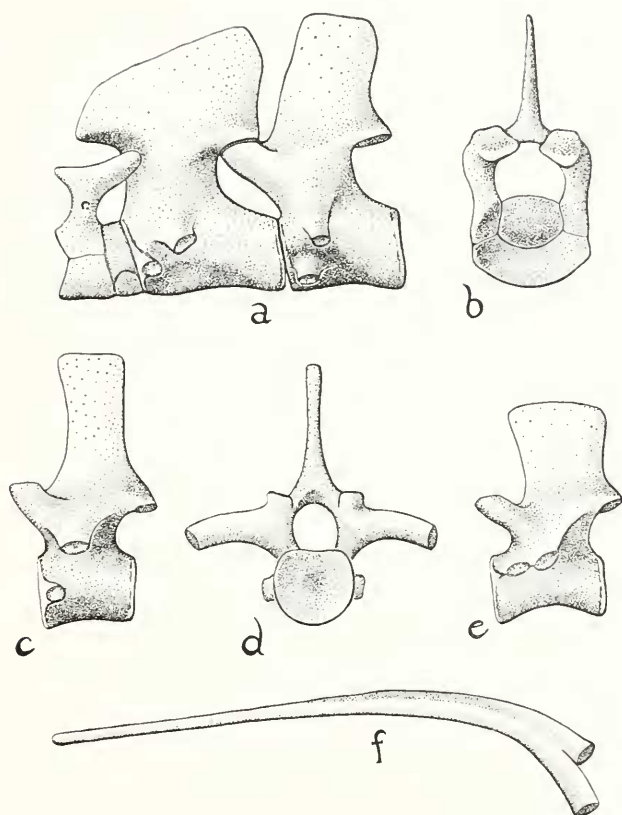


Figure 1. Vertebrae and rib of *Chanaresuchus bonapartei*. Composite, mainly from MCZ 4036. *a*, lateral view of vertebrae 1-3; *b*, anterior view of atlas-axis; *c*, *d*, lateral and anterior views of an anterior dorsal vertebra; *e*, lateral view of a posterior dorsal; *f*, an anterior dorsal rib, in postero-ventral view. $\times 1$.

articulate with the atlas intercentrum; internally it is excavated to form the dorsolateral segment of the socket for reception of the skull condyle. The lower part of this socket is formed by the atlas intercentrum, a stoutly developed crescent that articulates broadly on either side with the neural arches and is bevelled

anteriorly for condyle articulation. Behind the atlas intercentrum lies the axis intercentrum, a thin crescent connecting ventrally the atlas intercentrum and the axis centrum. The atlas centrum is a stout element, which forms the deeper part of the condylar socket (slightly indented centrally by a notochordal pit); dorsally it forms the anterior end of the floor of the neural canal; posteriorly it is firmly apposed to the axis centrum. It is partially obscured in lateral view by the atlas arch and intercentrum and ventrally by the axis intercentrum.

The axis neural arch is relatively low but long. As noted, the articulation of the atlas arch is simply a flattened area on the lateral surface of the arch, anteriorly; posteriorly, normal post-zygapophyses are present. A slight lateroventrally directed process, rugose at its tip, is an incipient transverse process for the tubercular articulation of the rib. The parapophysial articulation of the rib capitulum is indicated by a pronounced rugosity far down the side of the centrum and close to its anterior border. In contrast to the intercentrum anterior to it, the axis centrum (like the cervical vertebrae that follow it) is keeled ventrally.

Presacral column (Fig. 1, *c-e*). MCZ 4035 includes a presacral column and sacrum, showing definitely the presence of 23 presacral vertebrae; MCZ 4037 includes, in two segments, the 23 presacral vertebrae, the column having presumably broken off at the sacrum. Most of the description that follows is drawn from these two specimens; unfortunately, in much of both columns the transverse processes are broken and incomplete.

The column is, for the most part, of a typical thecodont character. In MCZ 4037 the length of typical dorsal segments, measured along the centra, averages 16 mm; in MCZ 4035, a somewhat smaller individual, this measurement averages 14 mm. The neural spines are centered somewhat to the back of the mid-length of the centrum; they are broadened anteroposteriorly, expanding in width above the region of the zygapophyses. The anterior spines are relatively tall and narrow; posteriorly, in the lumbar region, they are lower and broader distally. They are narrow in transverse diameter, without noticeable expansion at the top. When the surface is well preserved, faint longitudinal striations are frequently seen. In the larger specimens there appears to have been a late continuation of growth (or rather ossification) of the spines, the neural spines in larger forms being

taller in relation to other dimensions of the vertebrae. For example, in the large specimen, MCZ 4037, the total height of a posterior cervical (including both arch and centrum) is approximately three times the length of the centrum; in the smaller MCZ 4035, the height is barely above two and one-third times the central length.

The posterior zygapophyses are situated directly below the posterior margins of the neural spines; the prezygapophyses, on the contrary, lie well in advance of the anterior margins of the neural spines, on arch processes running upward and forward from the anterior margins of the transverse processes. The articular surfaces of the posterior zygapophyses face somewhat outward as well as downward; the anterior zygapophysial surfaces, in contrast, face inward as well as upward. Beginning with the axis, transverse processes are developed, their bases centering at a point well down on the side of the arch and toward the front. They are directed slightly posteriorly and ventrally rather than directly laterally. The axis process projects but 2 mm or so from the surface of the arch; posteriorly, the lengths increase so that, for example, by vertebra 7 in 4037, the length is close to 10 mm and there is obviously further increase more posteriorly, although, to my regret, the processes of the posterior dorsal and lumbar regions are mostly broken and imperfect. In MCZ 4035 the transverse processes as far back as vertebra 7 terminate in a narrow tip; posteriorly the transverse processes are broadened anteroposteriorly for their entire length, with oval distal facets for tubercular attachment.

The anterior margin of the arch curves almost directly downward from the process supporting the anterior zygapophysis to the anterior margin of the centrum; posteriorly the lateral margin of the arch is strongly concave in outline, allowing a large gap between arches here for passage of nerves and vessels.

The centra are smoothly oval in end contours, with a height considerably greater than the width. The centra are amphicoelous, with thickened rims at either end. Between the two ends of the centrum, the element pinches in somewhat laterally, and in side view the lower margin is somewhat concave in outline. The anterior centra are distinctly keeled ventrally; at about the beginning of the dorsal region the keel fades out, and posteriorly the ventral surface is smoothly rounded.

In the axis the parapophysis is merely a rugose area far down the anterior margin of the centrum. Posteriorly the parapophysis gradually moves upward along the anterior margin of the centrum and slowly comes to project distinctly from the surface of the bone so that, for example, by presacral 10 it has risen nearly to the top of the front margin of the centrum and projects outward for several millimeters. Posteriorly beyond this point the parapophysis continues movement upward and backward toward the transverse process and a thin ridge develops connecting the two (as in some primitive reptiles). Regrettably the processes are but imperfectly preserved in the "lumbar" region of materials available to me, but it appears that in the last four or so presacrals the two processes are united.

Sacral vertebrae. The two sacral vertebrae are present in MCZ 4035, and are present also in a Tucumán specimen. They differ mainly from the vertebrae anterior to them in the broad base from both centrum and arch from which the apophyses supporting the sacral ribs arise.

Caudal vertebrae. In the material available to me at Harvard, there is little identifiable caudal material; even in specimen MCZ 4035 articulated vertebrae cease at the third caudal. In the Instituto Lillo material, however, one specimen shows twelve caudal vertebrae in articulation with the sacrals and eleven are present in a second specimen. There is little decrease in vertebral length in these series of proximal caudals. Immediately behind the sacrum, however, the neural spines begin to show a backward slant and show a decrease in breadth distally; in the end members of these series, the neural spine is reduced to a small elevation lying above the postzygapophyses. Transverse processes are well developed; broad at their bases, they extend laterally and slightly ventrally to become pointed at their tips. In a Tucumán specimen of rather small size (skull length 175 mm), the lengths of the transverse processes of the anterior caudals, measured from the mid-line, are, in sequence, 29, 30, 28+, 33, 29, 25 and 20 mm. In this specimen the first chevron preserved lies between the fifth and sixth centra. That this is truly the first of the series is suggested by the fact that there is little space between the more anterior centra for insertion of a haemal arch, whereas more posteriorly a sufficient ventral gap is present. That the chevrons extended far down the tail is indicated by the fact that in the small

specimen mentioned below, they are seen in the region of the 20–23rd caudals.

In an Instituto Lillo specimen considerably smaller than “adult” specimens of *Chanaresuchus* but definitely representing a young individual of this form, 35 articulated caudals are present, plus a few disarticulated elements beyond. In its present condition, little detail can be made out, but the last elements appear to be subterminal in nature, and a length of 40 or so caudals seems to be indicated.

Ribs. Regrettably, there is no available specimen with a good set of articulated ribs. In two instances a single rod-shaped structure that appears to be a single-headed atlantal rib, is present at the anterior end of a column. Back of the atlas, the ribs are distinctly double headed in typical archosaur fashion. In the anterior part of the presacral column, the two heads are widely separated; in correlation with the rapid development of transverse processes as we progress backward, the capitular branch is much longer than the tubercular, curving downward and inward from the line of the shaft. A short series of articulated vertebrae in MCZ 4038, representing an individual somewhat smaller than the “adults,” bears a sequence of cervical ribs, presumably beginning with the atlas; the lengths are: 6, 12, 26, 32, 52, 60, ?, $75\pm$ and 85 mm. The more anterior, at least, of this series have pointed tips, indicating that they lay anterior to the point of rib connection with the (presumably cartilaginous) sternum. There is no indication in these cervical elements of an anterior “spur” from a point near the head of the rib that is found in crocodilians, and is highly developed in certain other thecodonts.

Of ribs in the dorsal region, remains are sparse. A number of rib heads show some variation in the amount of separation of tubercle and capitulum, those in which the two are less widely separated presumably coming from the posterior part of the region, in which transverse processes and parapophyses are approaching one another. In MCZ 4037 a complete rib (Fig. 1, *f*) is present close behind the eighth vertebra and may belong to that segment. Regrettably, no ribs are preserved in association with vertebrae of the “lumbar” region, in which shortened ribs were presumably present. For most of its extent the rib is slender; proximally, however, there is a slight expansion in the form of a thin flange posterior to the main proximal end of the shaft, which runs to the capitulum.

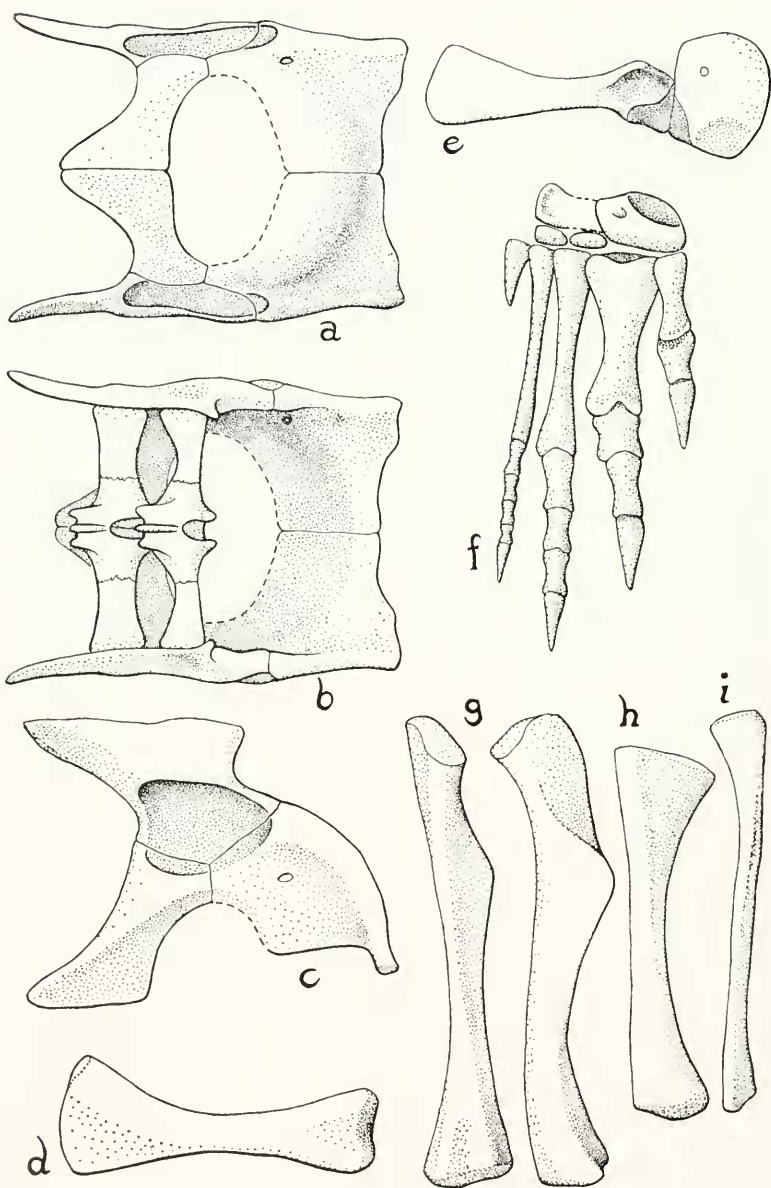


Figure 2. *Chanaresuchus bonapartei*, girdle and limb bones. Composite, but mainly from MCZ 4035. *a*, ventral view of pelvic girdle; *b*, dorsal view of pelvic girdle and sacral ribs; *c*, pelvic girdle from right side; *d*, left humerus, dorsal surface; *e*, right scapulocoracoid (dorsal end of scapula at left); *f*, right hind foot, calcaneum incompletely preserved; *g*, dorsal and lateral views of left femur; *h*, extensor surface of left tibia; *i*, extensor surface of left fibula. $\times \frac{1}{2}$.

Two sacral ribs are present in MCZ 4035, although some details are obscured. They extend outward from a broad base, including much of the lateral surface of the centrum as well as the lower part of the neural arch. They expand somewhat distally and are blunt-ended; as indicated by several specimens of ilia, they were not too firmly attached to the articular areas for them on the internal iliac surface.

Girdles. Several examples of scapulae and coracoids are present in available material; that illustrated (Fig. 2, *e*) pertains to MCZ 4035. The two elements of the endochondral girdle are not tightly sutured to one another, and were found separated in two instances. The scapula is tall and slender, somewhat broadened at its upper margin, which is a "finished" one in the specimens studied. At its lower end the scapula is somewhat expanded anteriorly and its margin curved outward, presumably for clavicular attachment. The posteroventral portion of the bone is thickened and bears externally the well-defined upper margin of the glenoid cavity, which faces posterolaterally. Scapula and coracoid meet in a long horizontal suture. The latter bone is an oval plate, thickened posterodorsally to bear the lower part of the glenoid, and having the usual coracoid foramen. The remainder of the bone is relatively thin and convex in contour externally, the lower portion obviously turning medially across the chest. There is no trend toward posteroventral expansion, such as would be expected in a possible crocodile relative. Presumably clavicles and interclavicles were present, but I have not been able to identify such elements in the material available.

A number of specimens include pelvic girdle material, so that the nature of the ilium, ischium, and the anterodorsal portion of the pubis can be readily recognized. In no case, however, is there present a complete, well-preserved pelvis with the elements in proper relations with one another. Closest to this condition is that associated with MCZ 4035, and my figured restoration (Fig. 2, *a-c*) is based on this specimen. Here the proper position of the ilia can be determined by their relation to the preserved sacral vertebrae and ribs; the ischia are for the most part well preserved; the pubes, however, are imperfect.

The ilium is of the primitive type seen in many thecodonts — essentially a simple vertical blade, extending posteriorly in tapering fashion some distance beyond the region of the acetabulum, the

front margin curving downward not far in advance of the acetabulum. On the inner surface are well-marked depressions for attachment of the two sacral ribs. On its outer surface the ilium forms the upper half of the acetabular cavity. This depression is most deeply incised posteriorly, where it reaches its most dorsal position, to be bordered dorsally by a sharp outwardly extending ridge on the ilium; thence the upper border, less sharply defined, slants forward and downward a considerable distance before reaching the pubis.

The pubis forms the anteroventral margin of the acetabulum; this cavity is here not as sharply incised into the bone as is true of its iliac and ischiadic margins, and the pubis is not greatly thickened here. The anterior surface of the ilium adjacent to the acetabular border is somewhat thickened; this surface continues downward to form a stout rounded ridge along the anterior margin of the pubis, the ridge turning ventrally in its distal portion. Medial to this ridge the pubis extends as a thin sheet to the mid-line of the body, where it meets its fellow in a long symphysis. Although the condition of the specimens makes the matter somewhat uncertain, it would seem that the anterior portion of this broad sheet of bone turns somewhat ventrally, while the posterior part of the symphyseal region lies in a horizontal plane.

At the posterior end of this ventral expanse of bone, the pubic symphysis terminates and the posterior margins of the two pubes retreat upward and outward toward the acetabular region. The exact nature of the posterior margin of the bone and the distance it retreats dorsally before making contact with the ischium is uncertain. The usual obturator foramen penetrates the pubis not far below the acetabular border.

The ischium forms the posteroventral sector of the acetabular border. The dorsal portion of the bone is here greatly thickened, forming a horizontal shelf with a crescentic outer margin, to constitute a prominent segment of the acetabular cavity. Below this area the ischium rapidly decreases in thickness, but increases in anteroposterior breadth ventrally. The posterior margin of the bone, slanting medially, descends nearly straight downward for some distance, then curves posteriorly and, finally, ventrally to meet its fellow in symphysis. This symphyseal union extends forward in a nearly horizontal plane to a point somewhat posterior

to the level of the puboischiadic area of contact below the acetabulum. Here, the symphysis terminating, the anterior margin of the ischium ascends nearly straight upward and laterally toward the acetabular region. We thus have, in *Chanaresuchus*, a definite advance in pubic structure over the proterosuchian condition in the presence of a broad ventral "incision" in the primitive puboischiadic plate and a marked break in the primitively continuous ventral symphysis.

Pectoral limb. Little material of the pectoral limb is available. A humerus, 85 mm in length, was found with MCZ 4035 (Fig. 2, *d*), but is not too well preserved. It is expanded at both ends in primitive reptilian fashion, but shows little of the primitive "twist" of one end on the other. The posterior margin of the "head" segment curves medially to the proximomedial corner of the bone, whence the proximal articular surface, facing dorso-medially, curves laterally around the head of the bone. At the proximal end of the lateral margin a typical deltopectoral crest is present (in crushed condition). The distal end of the bone is distinctly divided, both dorsally and ventrally, into medial and lateral condyles, the medial the stouter, with distal articular surfaces for radius and ulna. Neither of the foramina often present distally in the humerus of early reptiles is present.

I cannot with confidence identify either radius or ulna in any of the adult *Chanaresuchus* specimens studied. They are present, however, in association with a humerus in the small specimen in Tucumán, mentioned above. As preserved in this obviously immature individual, they are merely elongate bony cylinders, with some expansion proximally of the element which I take to be the ulna, but without indication of an olecranon. These elements, measuring 32 and 33 mm in length, are associated with a humerus measuring 36 mm in length. If the same proportions were to hold in MCZ 4035, the radius and ulna would be expected to measure 74 and 76 mm in length respectively.

Pelvic limb. The series of three major elements of the hind legs — femur, tibia, and fibula — are preserved in articulation in three instances, and a number of isolated hind leg elements are present on MCZ 4038. In the three articulated specimens the lengths of these elements as preserved are 128 mm, 94 mm, and 95 mm in MCZ 4035; $151 \pm$ mm, 129 mm, $91 +$ mm in the leg

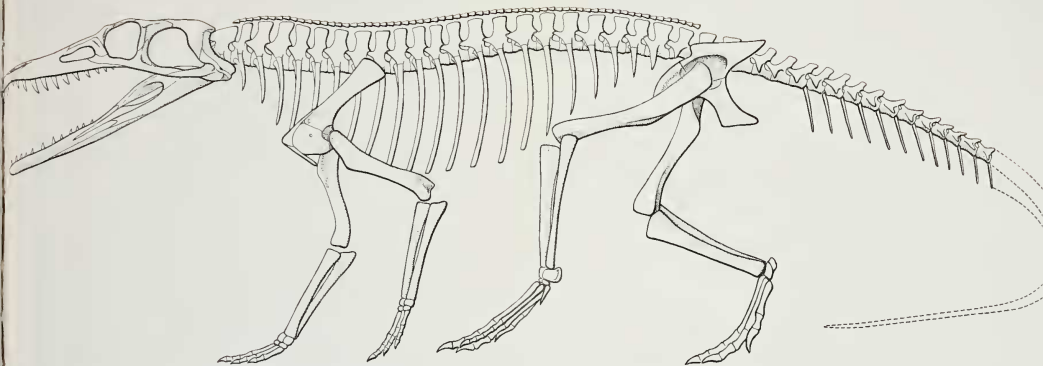


Plate 1. Skeletal restoration of *Chanaresuchus bonapartei*. Composite, but skull from the holotype, post-cranial skeleton mainly from MCZ 4035. Manus and dermal shoulder elements unknown; ribs imperfectly preserved and those of "lumbar" region unknown. About $\frac{1}{3}$ size of type and MCZ 4035.

of MCZ 4036 with articulated foot, $150\pm$ mm, 135 mm and 117+ mm for another specimen in the same block. As noted elsewhere, the skeleton of MCZ 4035 is apparently somewhat immature; the limbs in MCZ 4036 appear to be those of essentially mature individuals. In all three articulated examples the femur is definitely longer than the tibia; there is, however, a very considerable difference between the examples, in MCZ 4036 where the femoral length is 111 percent and 117 percent of the tibia, and MCZ 4035, where the figure is 135 percent.

The femur (Fig. 2, *g*) is of a pattern seen in many thecodonts and preserved little changed in crocodilians. The bone is relatively long and slender, the ends little expanded. In side view, the shape is sigmoid, with the proximal end curved upward and somewhat medially, the distal end curved somewhat downward; the curvature, however, is less extreme than in more advanced thecodonts. The proximal end of the bone is much modified, so that the morphologically medial (or anterior) margin is turned upward, the lateral border downward. The curved head of the bone is thickened, the thickening increasing toward the medial (upper) border; preservation in available material, however, is not good enough to clearly outline the articular area. About two-fifths the distance down, the bone is extended ventrally, with, medially, a large oval area that probably (as in crocodilians) lodged the insertion of the long caudifemoral muscle; the projecting lower margin is a trochanter that presumably afforded insertion to the caudifemoralis brevis. The bone broadens somewhat distally, with a partial division into condyles, a shallow intercondylar fossa above, and a ventral popliteal depression. The distal end of the bone is unossified in MCZ 4035, so that details of areas of articulation cannot be made out.

Tibia and fibula, again, are of typical primitive archosaur construction (Fig. 2, *h, i*). The broad head of the tibia is essentially triangular in section; there is little development of a cnemial crest, which is represented merely by the top of a ridge that descends much of the length of the bone, separating a lateral-facing surface of the shaft from one facing anteromedially. Terminally, there is a broad oval surface, somewhat convex, for articulation with the astragalus. The fibula is, as expected, a relatively slender element, somewhat expanded proximally for apposition to the femur; distally (in contrast with the situation in

many reptile groups) there is only a minor expansion in diameter of the bone to accommodate the oval terminal articulation with the calcaneum (and to a much lesser degree with the astragalus). Tarsal elements are present in MCZ 4035 and 4036. In 4035 the astragalus is well preserved (Fig. 2, f). Dorsally it bears a large articular area for the tibia, gently concave, elongate medio-laterally and facing somewhat anteriorly as well as dorsally, and dorsolateral to this a smaller facet for the fibula. No calcaneum was preserved with this specimen. MCZ 4036, on the other hand, lacks the astragalus, but has an incompletely preserved calcaneum. This shows a posterolateral tuber of "crocodilian" type, but the main body of the bone is imperfect. In both specimens mentioned distal tarsals 3 and 4 are present as flattened ovals lying over the heads of the lateral metapodials. There is no trace of more medial distal elements, although they may have been present in cartilage.

The structure of the pes is the most distinctive feature of *Chanaresuchus* (Fig. 2, f). Much of the right foot is present in MCZ 4035, but digit IV is represented only by a metatarsal splint; a right foot complete except for the ungual of toe IV is present in MCZ 4036, but the proximal ends of the inner toes are obscured by a refractory matrix. Two closely comparable specimens of the *Chanaresuchus* foot are present in the Tucumán material.

In archosaurs generally the trend in foot construction has been for a retention of the primitive phalangeal formula (except for frequent reduction of the fifth toe), but the development of a symmetrical pattern, with toe III the longest, toes II and IV somewhat shorter but subequal in length, and toe I short. This is true of the *Chanaresuchus* foot; but whereas in most archosaur toes II–IV are subequal in development, here there is very strong emphasis on the inner toes, and digit IV, on the contrary, is very slender. Digit I is somewhat shortened, but very stoutly built. Digit II is massive. Digit III is relatively slim. Digit IV is slender, almost splintlike in structure. Digit V is represented only by a metatarsal spur.

In some other archosaurs, such as certain crocodilians, *Ticinosuchus*, *Euparkeria* and *Stagonolepis*, there is a modest trend toward strength in the more medial digits, but never to an extent approaching the condition seen here. A similar trend (but usually a much less extreme one) towards a strengthening of the inner toes is found in mosasaurs and a number of chelonians. These

are aquatic forms, and this specialization is apparently an "improvement" in paddle-action—a fact that gives strength to the assumption that *Chanaresuchus* was in great measure a water dweller. It has been assumed that *Chanaresuchus* and its relatives in the Proterochampsidae might be antecedent to the Crocodilia, but such strong emphasis on the inner toes is not to be expected in an ancestor of the group. As regards possible phytosaur relationship, foot material of that group is rare, and the pes, when restored, is generally based on poor material. I am indebted to Dr. Chatterjee, of the Geological Study Group of the Indian Statistical Institute, for a figure of a well-preserved foot of a phytosaur from the Maleri Formation. This shows almost no trace of emphasis on the inner toes, and relationship of the Proterochampsidae to the phytosaurs seems highly improbable.

Dermal armor. No gastralia are present in articulated fashion in any specimen. In contrast to a large fraction of the thecodont assemblage, other body armor appears to have been feebly developed, and consisted merely of a single row of thin scales lying over the neural spines. As preserved in several specimens, scales are definitely present from the axis to the last presacral; there is no evidence as to whether they extended onto the tail region, although this was probably the case. The scales are wedge-shaped as seen from above, narrow anteriorly, broader posteriorly, with a low longitudinal median keel. The anterior end of each scale underlies that anterior to it. There are approximately three scales the length of each vertebra, although there is no apparent relationship between vertebral segmentation and scale arrangement; in one specimen 57 scutes were present above the first 20 vertebrae. Their appearance and arrangement is very similar to that pictured in *Ticinosuchus* by Krebs (1965, fig. 8). This author restores the dorsal scales in the presacral region in a double row, in analogy, I suspect, with the pattern seen in various other thecodonts. I doubt if this was the case. The scales preserved in the presacral region number only about enough to make up a single median row. The presence of scales above the tail vertebrae in *Ticinosuchus* suggests that, were appropriate materials to be discovered, they would be found to continue along the tail in *Chanaresuchus* as well.

Restoration. In the accompanying plate I have attempted a skeletal restoration of *Chanaresuchus* at one third the natural size

of a typical adult. Much of the skeleton is taken from MCZ 4035. The dermal shoulder elements, the manus, and the posterior ribs are restored, and the tail is imperfectly known. Despite these lacunae and the fact that in ribs and certain other elements the restoration is composite, I believe that the restoration gives a fairly accurate picture of the animal's skeleton.

In restoring an early archosaur, an important question is whether the pose was that of a biped or a quadruped. In all primitive reptiles the front legs are somewhat shorter and less massive than the hind. In most archosaurs this disproportion in limb lengths is usually much greater and led to a general (but not universal) belief (which I shared) that archosaurs *ab initio* were more or less bipedal in locomotor tendencies, and that most quadrupedal archosaurs, such as the sauropods and various ornithischians, had relapsed from a bipedal mode of progression back to progressing on all fours. Charig, Attridge and Crompton (1965) have, as a result of a study of probable sauropod history, come to the conclusion that quadrupedal pose was primitive for archosaurs, and that the development of powerful hind legs and a highly developed tail were, to begin with, adaptations for an amphibious life, and that bipedalism arose later.

It is not unreasonable to believe that, as these authors argue, the sauropods developed without passing through a bipedal stage. I think, however, that on present evidence, the primitive ornithischians were at least partially bipedal, although a majority of the ornithischian subgroups later became quadrupedal.

The possibility that the ancestral archosaurs were amphibious leads to speculation as to the general nature of early reptilian history. I have argued (although not without strenuous opposition) that the ancestral reptiles, although having acquired an amniote style of development, were still amphibious, and perhaps even mainly aquatic in habits. Of the great group of synapsids, which were dominant in the Permian and earlier Triassic, most became fully terrestrial, but the most primitive (and oldest) synapsids, the ophiacodont pelycosaurs of the Pennsylvanian and early Permian, were still essentially aquatic fish-eaters. Ancestral Permian archosaurs are almost unknown, but they may have followed a similar life pattern, but for a longer period of time. Further, we have no undisputed knowledge of the early ancestors

of the euryapsid sauropterygians and placodonts or of the ichthyosaurs; at their earliest appearance these reptiles were aquatic — and perhaps primitively so. *Mesosaurus*, of the Permo-Carboniferous boundary, shows that if the primitive reptiles had become terrestrial, reversion to the water took place at a very early stage of reptilian history. And while I do not want to even suggest any close relationship between archosaurs and *Mesosaurus* (whose phylogenetic relationships are quite problematical), the similar adaptations in this genus and in the archosaurs in the powerful tail and highly developed hind limbs are strikingly suggestive.

But to return from this discussion to the question of limb disparity and body pose in archosaurs. Correlation between limb proportions and presumed posture is none too simple a matter. Such obviously amphibious and quadrupedal forms as crocodilians and phytosaurs have front legs nearly as well developed as hind; in a "sample" crocodilian, for example, the humerus plus radius are about 84 percent the length of femur plus tibia, and in a phytosaur described by McGregor (1906), the figure is 87 percent. But forms that seem quite surely quadrupedal may show a considerably greater disparity in length between front and hind legs. The heavily armored aetosaurs, for example, are universally considered to be quadrupeds, but in *Aetosaurus* and *Stagonolepis*, according to figures given by Walker (1961), the front legs are but 61 percent and 64 percent the length of the hind. *Proterosuchus* [*Chasmatosaurus*] is an early and surely primitive thecodont that is reasonably regarded as amphibious in habits although the available materials suggest that the front legs were but about 66 percent the length of the hind.

On the other hand, *Euparkeria*, *Hesperosuchus*, and *Ornithosuchus* are regarded by those who have studied them (Ewer 1965, Colbert 1952, and Walker 1964) as bipedal; and yet their limb ratios are as high or higher than some of the presumed quadrupeds, being 70 percent, 67 percent, and 70 to 75 percent, respectively. Obviously limb proportions in themselves are not sufficient to enable one to give a firm conclusion as to pose; body structure in general must be taken into consideration.

As regards *Chanaresuchus*, the limbs are very markedly disproportionate. If the radial length in MCZ 4037 was that estimated in relation to the humerus, the front leg would be but 53 percent that of the hind. However, the humerus of this specimen

may be incomplete distally. If, instead, we take the small specimen from Tucumán in which all four bones conceived are present (with lengths of 39 mm for humerus, and 32, 59, and 59 for radius, femur, and tibia), we get a somewhat higher figure of 61 percent. These figures taken by themselves would seem to strongly suggest bipedality. But in other regards there is considerable reason to believe that *Chanaresuchus* was amphibious, spending much of its time in the water, where the body would be in a horizontal position; and while the animal could quite probably assume a semi-erect bipedal posture, this would only occur at such times when, ashore, speed seemed imperative. In consequence, I have restored the animal as a quadruped.

Relationships. In the preceding paper of this series, I have commented on possible relationships of *Chanaresuchus* and its relatives in the Proterochampsidae. Reig (1959) and Sill (1967) have argued for *Proterochampsia* as a pre-crocodile; Walker (1968), on the other hand, maintains that this genus is a pre-phytosaur rather than a pre-crocodylian, but maintains that its "cousin" *Cerritosaurus* is pre-crocodylian. Study of skull structure led me to believe that there was little in the cranial anatomy of *Chanaresuchus* to suggest relationships to either Crocodylia or Phytosauria, and that this group, the Proterochampsidae, was essentially a sterile one, representing a modest advance over the Proterosuchia, which in middle Triassic days occupied a position in the ecology similar to that of the phytosaurs of the late Triassic and the crocodylians of the later Mesozoic. Study of the postcranial anatomy does not lead me to change my previous conclusions.

The postcranial skeleton is for the most part of a primitive and generalized archosaurian type; the only advances over the proterosuchian condition lie in the fact that the pelvis has progressed to a more typical archosaurian condition in the "cleavage" between pubes and ischia for much of their height, with interruption of the primitively continuous ventral symphysis, and in the initiation of body armor not found in known proterosuchians. The armor is very lightly developed — much less than we would expect in an Anisian(?) predecessor of either crocodylians or phytosaurs. The pubis shows no indication of a trend toward exclusion from the acetabulum, as one might expect in a crocodile ancestor. The cervical ribs lack the specialization seen in crocodylians (and certain other thecodonts) of an anterior "spur" near the head.

Still further, the pes is of a highly specialized nature, not of a type antecedent to either crocodilians or phytosaurs.

Gualosuchus postcranial material. I may note that a small amount of postcranial material was found with the type skull of *Gualosuchus*; this included a scapulocoracoid, femur, parts of two tibiae, and a few bones of the pes. The elements preserved are in general comparable, except for larger size, to those of *Chanaresuchus*. The anterior border of the scapula is less everted than in *Chanaresuchus*. The height of the scapulocoracoid is 148 mm, the femoral length 158 mm. The femoral length is close to 50 percent the overall length of the skull, indicating that the *Gualosuchus* skull was rather shorter in proportion to body measurements than that of the relatively long-snouted *Chanaresuchus*. Further postcranial remains of *Gualosuchus*, which I trust will be described presently by Sr. Bonaparte, are present in the Instituto Lillo collections. In one specimen in that collection the humerus is somewhat less than two-thirds the length of the femur, thus indicating the same disproportion in limb length as in *Chanaresuchus*.

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